

European and North West African Lycaenidae (Lepidoptera) and their associations with ants



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Abstract. The information about ant-associations of European and North West African lycaenid caterpillars is summarized. A tentative classification of the different degrees of myrmecophily is proposed. More than 75 % of the species considered are myrmecophilous. In the Polyommatus, even more than 90 % are ant-associated. An apparent correlation between the ant-association of lycaenids and their systematic position is discussed. This is contradictory to a recent work that suggested a much lower proportion of myrmecophilous species in the Western Palaearctic region and rejected any connections between lycaenid phylogeny and myrmecophily.

Introduction

The association of lycaenid larvae and ants, termed myrmecophily, has been the subject of extensive research. During the last decade, in particular, a number of papers concerned with the physiology, ecology, and evolution of lycaenid myrmecophily have been published (e.g. Pierce, 1983, 1985, 1987; Pierce and Mead, 1981; Pierce and Eastseal, 1986; Henning, 1983 a & b; Cottrell, 1984; Fiedler and Maschwitz, 1988 a & b, 1989 a & b). However, a comprehensive compilation of all information regarding lycaenid myrmecophily from a single biogeographical area has not yet been undertaken. In 1969, Malicky listed the ant-associations of European species recorded until then, but in the past 20 years considerable progress has been made in the investigation of larval life-histories, adding numerous records of ant-larvae associations. Thus, it seems justified to summarize the current knowledge of Western Palaearctic lycaenids and their ant-associations, to point out the still significant gaps in our knowledge, and to discuss the results in the light of the recent research on myrmecophily and, in particular, the biogeographical and evolutionary hypotheses of Pierce (1987).

In the present paper I have attempted to gather all available, but scattered information on ant-associations and the presence of myrmecophilous organs in European and North West African lycaenid species. Important sources of data were the most useful review papers of Warnecke (1932/33), Hinton (1951), Malicky (1969), and Kitching and Luke (1985). Further information was derived from the books of Weidemann (1986, 1988) and SBN (1987), but special efforts were devoted to sample data from original sources, e.g. numerous journal papers and observations of several colleagues. Despite my efforts to approach completeness, the

following list is certainly still far from being complete, and further additions will be welcome.

Methods

In the present study I have considered all lycaenid species known from Europe and North West Africa north of the Sahara desert as listed in Higgins and Riley (1978) and Kudrna (1986), and the available information regarding the presence of myrmecophilous organs and ant-associations was compiled. The systematic arrangement basically follows Scott and Wright (1990). Thus, the "Theclinae" sensu Eliot (1973) are regarded as paraphyletic and are replaced by the (more likely monophyletic) tribes *Aphnaeini*, *Theclini*, and *Eumaeini*. The former subfamilies *Lycaeninae* and *Polyommatainae* are likewise downgraded to tribal level, i.e. *Lycaenini* and *Polyommattini*, respectively. The phylogenetic relationships of these tribes to each other, as well as to the other lycaenid subfamilies (*Poritiinae* including *Liptenini*; *Miletinae* including *Liphyrini*; *Curetinae*) are not yet sufficiently established. Indeed, some of the taxa considered here strongly need further confirmation as monophyletic groups. Because a more satisfactory phylogenetic higher classification of the Lycaenidae is not yet available, the arrangement adopted here is necessarily tentative.

The Riodinidae (with the single European species *Hamearis lucina* L.) are treated as a separate family, their associations with ants being based on the convergent evolution of structurally different ant-organs (see Cottrell, 1984; DeVries, 1988 & 1990) which occur only in the most apomorphic tribes *Eurybiini*, *Lemoniini*, and *Nymphidiini* (Harvey, 1987). It is important to stress that riodinid myrmecophily should be discussed as a phylogenetically separate and functionally convergent phenomenon when compared with ant-associations of the Lycaenidae (DeVries, 1990).

Nomenclature and taxonomy largely follow Kudrna (1986) with only minor deviations. The subgenera of the genus-groups *Plebejus* and *Polyommatus* are basically treated as in the paper of Zhdanko (1983). Exceptions are the taxa *Eumedonia* (here included in *Aricia*), *Lysandra* (including *Plebicula* sensu Higgins and Riley, 1978) and *Meleageria* (both as subgenera of *Polyommatus*). The generic classification within most groups still strongly requires a phylogenetic analysis.

The species concept is in most cases adopted from Higgins and Riley (1978) and Kudrna (1986). Exceptions are, for example, the *Plebejides* and *Lysandra* groups (after Schurian, 1989, Bálint & Kertész 1990) and a few taxa of *Agrodiaetus*. In the latter subgenus, a number of taxa has been described from the Mediterranean area solely based on chromosome studies, but their taxonomic status needs further investigations. In general, subspecies and local forms are not considered separately, but highly isolated endemic forms (e.g. from several southern European mountain areas) are treated as distinct species (instead of vicariant subspecies) because of their genetic separation.

Based on the records available, I have tentatively assigned the degree of larval myrmecophily to each species where possible. This assignment is based primarily on field records, laboratory experiments are considered only exceptionally. The scoring is as follows:

0: not ant associated: **myrmecoxenous**.

1: very few ant-associations reported, stable ant-associations formed only exceptionally: **weakly myrmecophilous**.

2: a varying proportion of larvae attended by ants, intermediate between 1 and

3: **moderately myrmecophilous**.

3: most if not all mature larvae ant-associated: **steadily myrmecophilous**.

4: larvae dependent on ants as commensals (*Cigaritis*) or parasites (*Maculinea*): **obligately myrmecophilous**.

Usually the scorings in Table 1 refer to the larvae. Where the pupae are known to have a different stage of myrmecophily, this is indicated separately.

The presence of larval myrmecophilous organs is represented in Table 1 as follows: two asterisks (**) indicate a complete set of ant-organs (a dorsal nectary organ (DNO) plus a pair of eversible tentacle organs (TOs)); one asterisk means that only a DNO is present (sometimes only rudimentary, e.g., *Callophrys*: Fiedler 1990b). Species without an asterisk possess only pore cupola organs (PCOs) (see Cottrell, 1984 and Fiedler, 1988 for terminology, details and references).

When the figures indicating the degree of myrmecophily, or the asterisks referring to the equipment with ant-organs are bracketed, the respective assignments are hypothetical. In these cases the assignment is based on the status of closely related species (example: in *Agrodiaetus* the early instars of only a few species are well-known and all are highly ant-associated; judging from the close affinity between these taxa, it seems very likely that all *Agrodiaetus* caterpillars possess a full set of myrmecophilous organs and are steadily myrmecophilous).

Where possible from the records available, the ant genera and/or species involved in myrmecophilous interactions are listed. It has to be emphasized that many determinations were not checked by ant specialists, thus several old records are reliable only on genus level. For example: *Lasius "niger"*, "*alienus*", and "*flavus*" all are complexes of several closely related ant species which are nearly indistinguishable for the non-myrmecologist (e.g. Seifert, 1988 and pers. comm.). The term "indet." means that ant-associations have been observed but the ants involved were not determined. A question mark (?) indicates that ant-associations are likely, but no certain information is available. The dash (—) means that ant-associations have never been reported for the respective lycaenid species.

Regarding the sources of data, I have listed the review papers and books as references where appropriate to facilitate use. Special journal articles and personal communications are only cited when the information in the major references is incomplete or even incorrect. Purely descriptive papers (e.g. rearing records) are excluded except when they yield the only information about the presence or absence of ant-organs. Similarly, laboratory observations on myrmecophily are only considered when no sufficient field data are available. For most species the knowledge is still far from being complete. In several cases (species from Southern Europe) only information from outside Europe (e.g. Africa) is available, and for a few taxa there is no information regarding the larval biology at all (see footnotes to Table 1).

The information sampled in Table 1 is used for a quantitative analysis to determine the number and proportion of myrmecophilous species in the Western Palaearctic fauna. In Table 2a only those species are considered where appropriate information on the larval biology, including direct (positive or negative) evidence concerning myrmecophily, is present. In Table 2b, in addition, all species are included where at the current stage of our knowledge a reasonable

hypothetical assignment can be made (based on the presence of myrmecophilous organs and/or the state of the closest relatives). In accordance with experimental work (e.g. Fiedler and Maschwitz, 1989a, Fiedler, 1990a), the presence of a functional DNO is considered to indicate a facultative ant-association at least, while in species without ant-organs (DNO and TOs) such associations are supposed to be non-existent or weakly developed at most.

Results and Discussion

In Table 1 the European and North West African lycaenid species are listed together with the information about their ant-associations. The first column contains the species name, the second column gives the tentative assignment of the degree of larval myrmecophily. In the third column the ant genera or species involved are given, and the last column contains the source of data. Table 2 summarizes the absolute numbers and percentages of myrmecophilous species.

It is apparent from the Tables 1 and 2 that, in the Western Palaearctic region, the vast majority (more than 75 %) of lycaenid species are myrmecophilous at least towards the end of the larval stage. This conclusion can be drawn from either direct evidence (Table 1, 2a) or hypothetical assignments (Table 2b), which both yield almost identical figures. Thus there is a marked contrast to the results of Pierce (1987), who stated that only 30 % of the European species (32 % of the genera) are myrmecophilous. The reason for this difference is the incomplete evaluation of literature records: Pierce's data are derived solely from the review papers of Malicky (1969), Kitching and Luke (1985), and identification guides like Higgins and Riley (1978).

On the grounds of her data, Pierce (1987) concluded that there is a difference in the proportion and obligateness of ant-associated lycaenids between the northern and southern hemisphere, the latter having 70-90 % myrmecophilous species, the former only 20-40 %. From the results presented here it becomes obvious that this disparity does not exist for, at least, the proportion of myrmecophily in Europe; instead, the figures in Table 2 are close to those for the southern hemisphere given by Pierce. In Japan, the proportion of myrmecophilous species is about 56 %, but this rather low figure is mainly due to the preponderance of myrmecoxenous *Thecliti* there (Fiedler, 1990 a). The systematic structure of the Japanese lycaenid fauna is thus not representative for the whole Eastern Palaearctic region. From the Nearctic region a considerably smaller proportion of myrmecophilous species has been definitely recorded (about 30 %: Fiedler, 1990 a), but this awaits further confirmation (see Ballmer and Pratt, 1988).

Whether the degree of myrmecophily does show a north-south disparity remains to be clearly demonstrated. In the Western Palaearctic region only few species in the genera *Maculinea* (Thomas et al., 1989) and *Cigaritis* (Rojo de la Paz, 1990) are known to be obligately myrmecophilous. Recent observations on *Plebejus argus* and *P. (Lycaeides) idas* in

Europe, however, suggest that both are obligatorily and specifically associated with certain ants (*Lasius* species from the *niger* and *alienus* groups in the case of *P. argus*, species of the *Formica cinerea* group in the case of *P. idas*; see Mendel and Parsons, 1987, Jutzeler, 1989c & d, 1990, Ravenscroft, 1990). In the tropics detailed studies on lycaenid-ant interactions are still rather sparse. Only from South Africa (e.g. Clark and Dickson, 1971, Henning, 1983a, b) and from Australia (Common and Waterhouse, 1981) sufficient information is present on a larger number of species, while in South Asia most records are merely anecdotal (cf. Corbet and Pendlebury, 1978), and the life-histories of Neotropical Lycaenidae are largely unknown. The data from South Africa indeed suggest a high proportion (about 50 %) of obligatorily myrmecophilous lycaenid species, largely due to the great diversity of the tribe Aphnaeini (*Aloeides*, *Poecilmitis* etc.) and the genus *Lepidochrysops* in Africa. In Australia, the *Lucia* and *Zesius* sections of the Theclini contain a rather high number of obligate myrmecophiles (> 30 % of all Australian lycaenids), whereas the situation in South Asia appears to be intermediate (10-20 % obligate myrmecophiles; Fiedler, 1990 a). Thus, the current stage of our knowledge does not conclusively support Pierce's hypothesis concerning the general north-south disparity in the obligateness of lycaenid-ant interactions. Rather the high proportion of obligate myrmecophiles among the lycaenids of South Africa and Australia may reflect the peculiar history of the latter 2 areas (Fiedler, 1991).

In Europe, most lycaenids are associated non-specifically with a variety of ant species, often from different subfamilies. Only about 10 species from the genera *Cigaritis*, *Maculinea* and *Plebejus* maintain species- or at least genus-specific relationships with ants (see above). As was already pointed out by Malicky (1969), the dominance structure of the ant fauna in the larval habitats is decisive for which ant species actually tends a lycaenid caterpillar. In fact, members of any ant genera that maintain trophobiotic relationships with other organisms producing nutritive liquids (e.g. homopterans, myrmecophytes) are likely to attend myrmecophilous lycaenid larvae (DeVries, 1991). Because of the general dominance of Formicinae ants in temperate regions (e.g. Seifert, 1986; Fellers, 1987, 1989) it is not surprising that the dominant trophobiotic formicine genera *Lasius* (recorded with 23 lycaenid species), *Formica* (14 species), *Camponotus* (10 species) and *Plagiolepis* (10 species), as well as *Tapinoma* (Dolichoderinae; with 12 lycaenid species), *Myrmica* (Myrmicinae; 20 species) and *Crematogaster* (10 species) are mentioned most often in Table 1.

Although the higher classification of the Lycaenidae is not yet resolved, another pattern is apparent from the results above: There is a strong correlation between systematic position and myrmecophily (Fiedler, 1990a). Most members of the Lycaenini, for example, have no ant-associations, presumably due to the absence of a dorsal nectary organ. Only for one European species, *Lycaena dispar*, there exist old records of

ant-associations, while the remaining 12 European species appear to be myrmecoxenous. In North America only 4 out of 15 species of the genus *Lycaena* are with certainty known to associate with ants with the help of specialized dendritic setae (Ballmer and Pratt, 1988). Ant-associations are unknown from African and New Zealand *Lycaena* (Clark and Dickson, 1971, Gibbs, 1980), from Asian *Heliothis* (Eliot, pers. comm.) and from Papuan *Melanolycaena* (Sibatani, 1974). Thus, the Lycaeninae as a whole seem to be a myrmecoxenous group with only few secondary exceptions.

The Polyommatini show the reverse pattern: nearly all European species are ant-associated (Table 1), the only exceptions being the subgenera *Agriades* and *Vacciniina*. Both occur in arctic or alpine tundra, or wet boreo-montane bogs with limiting nutritional resources and few ant species present. The Polyommatini of Africa, Australia, and North America also contain a large number of myrmecophilous species (e.g. Clark and Dickson, 1971, Common and Waterhouse, 1981, Ballmer and Pratt, 1988) with rather few exceptions (e.g. desert species, lycaenids with endophytic larvae). Thus, the Polyommatini are basically ant-associated and reductions of myrmecophily (and ant-organs) have occurred in only a few species that occur where the ecological conditions did no longer favor the symbiosis with ants.

The predominantly African tribe Aphnaeini is another strongly myrmecophilous group: the high proportion of obligately myrmecophilous species in South Africa is mainly due to the Aphnaeini genera *Aphnaeus*, *Apharitis*, *Spindasis*, *Aloeides*, *Phasis*, *Poecilmitis*, and the polyommatine genus *Lepidochrysops* (Clark and Dickson, 1971; Claassens and Dickson, 1980). The only representatives of the Aphnaeini in the Palaearctic region (genus *Cigaritis*) are specifically associated with ants of the myrmicine genus *Crematogaster* (Rojo de la Paz, 1990).

The remaining and rather heterogeneous tribes Theclini and Eumaeini show different pictures. The Theclini contain a large number of ant-associated species in South Asia, Africa, and Australia (Clark and Dickson, 1971, Corbet and Pendlebury, 1978, Common and Waterhouse, 1981). The 3 European species as well as the 2 North American members of this tribe, however, belong to the mainly Sino-Oriental subtribe Thecliti, and this whole subtribe has apparently reduced its ant-associations. Possibly the Thecliti (as the temperate-zone sister-group of the Arhopaliti, a basically Oriental ant-associated lineage) reduced their myrmecophily when adapting towards temperate regions. In South East Asia and Australia, the Theclini subtribes Luciti, Zesiiti, Ogyriti, and Arhopaliti are predominantly myrmecophilous, including a number of obligately ant-associated species (e.g. Common and Waterhouse, 1981, Fukuda et al., 1984, Fiedler, 1990a).

The tribe Eumaeini sensu Scott and Wright (1990) is the largest of the whole family Lycaenidae. Myrmecophily and myrmecophilous organs are known from its subtribes Amblypoditi, Catapaecilmatiti, Loxuriti,

Iolaiti, Deudorix, and Eumaeiti (Fiedler, 1990a). In Europe there are only a few representatives of the genus *Tomares* and the subtribe Eumaeiti. The *Tomares* species possess a complete set of ant-organs and are facultatively ant-associated. *Tomares* belongs to the Deudorix (Eliot, pers. comm.) which subtribe contains a number of myrmecophilous species in the tropics (e.g. Clark and Dickson, 1971).

The Eumaeiti are most diverse in America (Eliot, 1973) including the species-rich genera *Callophrys*, *Strymon*, *Satyrium*. In the Palaearctic region, comparatively few species (< 60) of the genera *Satyrium* s. l. and *Callophrys* s. l. occur (Bridges, 1988). Within the genus *Satyrium* there appears to be a marked tendency to reduce ant-associations, and this is even more pronounced in *Callophrys* where only very few species have been found to be tended by ants. Interestingly, both genera lack the tentacle organs (Ballmer and Pratt, 1988), and the dorsal nectary organ ("honey gland") - though present - does not secrete nutritive liquids in some species (e.g. *Callophrys rubi*, Fiedler, 1990b). Hence, the Eumaeini of the temperate regions seem to be a tribe with a basically low level of myrmecophily and a high tendency to further reduce ant-associations and the related organs. Unfortunately the current knowledge of the biology of neotropical Eumaeiti is still too fragmentary to support further interpretations. The ecological regimes selecting for the parallel reduction of myrmecophily in the Theclini and Eumaeini are not as clear as in the Polyommatus. Possibly the preference for rather nutrient-poor food-plants of the families Fagaceae, Betulaceae, Salicaceae and others may play a role, together with the generally lower diversity and abundance of ants in temperate woodlands (Jeanne, 1979), resulting in a lower chance of maintaining stable trophobiotic associations there. Most of the Palaearctic Polyommatus species, in contrast, occur in open habitats which support a more diverse ant fauna (Seifert, 1986). Clearly further studies are required on this interesting evolutionary feature.

It is now relevant to assess the importance of these results with respect to the biogeography of lycaenid myrmecophily. Apparently the systematic composition of the lycaenid fauna of the biogeographical regions largely influences the proportion and obligateness of myrmecophily. The lycaenid fauna of Europe, for example, is predominated by species of the Polyommatus (72 %), resulting in a high proportion of (at least facultatively) ant-attended lycaenids. The Lycaenidae fauna of North America, in contrast, contains a higher percentage of Eumaeiti and Lycaenini species (67 % of the resident species). Not surprisingly, the proportion of myrmecophily is lower. Among the African lycaenids, two thirds of the fauna belong to the Aphnaeini, Old World subtribes of the Eumaeini, and Polyommatus: Most of these species are myrmecophilous. The remaining third are species of the Poritiinae whose larvae in most cases do not maintain close ant-associations (Clark and Dickson, 1971).

Thus, contradictory to the conclusions of Pierce (1987: "The distribution of ant association within the Lycaenidae is independent of phylog-

eny"), this study suggests a high correlation between lycaenid phylogeny and the evolution of myrmecophily. It also suggests that this systematic effect may significantly influence the biogeography of lycaenid-ant-associations. Notwithstanding the uncertainties of lycaenid systematics, a substantial discussion of the biogeography and evolution of lycaenid myrmecophily can hardly be realized without a phylogenetic approach. Much more work needs to be done on the higher classification of the Lycaenidae as well as in the description and analysis of larval life-histories and ant-associations in all biogeographical regions to confirm or reject the hypotheses given above. This paper is a first attempt to understand a small region (Europe), and is intended to stimulate broader and more thorough analyses.

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Table 1: List of species, degree of myrmecophily, and associated ants of European and North West African Lycaenidae and Riodinidae. Only field records are included except where stated otherwise (lab.). Further explanations see text and footnotes.

Species	Degree of myrmecophily	Ant species involved	Source of information
Riodinidae			
<i>Hamearis lucina</i>	0	—	Malicky 1969b (lab.) Fiedler 1990a
Lycaenidae			
<i>Aphnaeini:</i>			
<i>Cigaritis zohra</i>	4**	<i>Crematogaster laestrygon</i>	Rojo de la Paz 1990
<i>C. allardi</i>	3**	<i>Crematogaster auberti</i>	Rojo de la Paz 1990
		<i>C. antaris</i>	
		<i>C. scutellaris</i>	
<i>C. siphax</i>	(3/4**)	?	no record
<i>C. acamas</i>	4**	<i>Crematogaster</i> sp.	Larsen & Pittaway 1982
<i>C. myrmecophila</i>	4**	<i>Crematogaster auberti</i>	Hinton 1951
		<i>Cataglyphis bicolor?</i>	
<i>Lycaenini:</i>			
<i>Lycaena phlaeas</i>	0	—	Kitching & Luke 1985
<i>L. helle</i>	0	—	SBN 1987
<i>L. dispar</i> ^a	0/1?	<i>Myrmica rubra</i>	Hinton 1951
<i>L. virgaureae</i>	0	—	SBN 1987
<i>L. ottomanus</i> ^b	(0?)	—	Elfferich, pers. comm. (lab.)
<i>L. tityrus</i>	0	—	SBN 1987
<i>L. alciphron</i>	0	—	SBN 1987
<i>L. hippothoe</i>	0	—	SBN 1987
<i>L. candens</i>	(0)	—	no record
<i>L. thersamon</i>	0	—	Larsen 1990
<i>L. phoebus</i>	0	—	Rojo de la Paz, pers. comm.
<i>L. thetis</i>	(0)	—	no record
<i>L. ochimus</i>	(0)	—	no record

Theclini:

<i>Thecla betulae</i>	larva: 0/1 pupa: 3	<i>Lasius niger</i> (pupa)	Malicky 1969b, Kitching & Luke 1985, Emmet & Heath 1990
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<i>Laeosopis roboris</i>	(1?) [*]	?	Agenjo 1963
<i>Quercusia quercus</i>	larva: 0/1 pupa: 2	<i>Lasius</i> sp.? (pupa)	Kitching & Luke 1985, Emmet & Heath 1990

Eumaeini:

<i>Tomares ballus</i>	2 ^{**}	<i>Plagiolepis pygmaea</i> + indet.	Chapman & Buxton 1919, Malicky 1969b, Jordano et al. 1990
<i>T. mauretanicus</i>	(2) ^{**}	?	Malicky 1969b
<i>T. nogelii</i>	3(**)	indet.	Hesselbarth & Schurian 1984
<i>Callophrys rubi</i> °	larva: 0/1* pupa: 2	??	Malicky 1969b, Fiedler 1990d, Emmet & Heath 1990
<i>C. avis</i>	(0)*	—	Dujardin 1972
<i>Satyrium w-album</i>	2*	indet.	Malicky 1969b, Kitching & Luke 1985, Schurian, pers. comm.
<i>S. spini</i>	2*	indet.	Malicky 1969b
<i>S. ilicis</i>	2*	<i>Camponotus aethiops</i>	Malicky 1969b, SBN 1987
<i>S. esculi</i>	2*	<i>Camponotus cruentatus</i>	Martín & Gurrea 1983
<i>S. acaciae</i>	0*	—	Schurian, pers. comm.
<i>S. (Fixsenia) pruni</i>	0	—	Kitching & Luke 1985

Polyommatini:*Jamides* section

<i>Lampides boeticus</i>	2 ^{**}	<i>Lasius niger</i> <i>Camponotus compressus</i> <i>C. cruentatus</i> <i>C. sylvaticus</i> <i>C. foreli</i> <i>Prenolepis clandestina</i> <i>Plagiolepis</i> sp. <i>Tapinoma melanocephalum</i>	Hinton 1951, Martín Cano 1984; Schurian & Wiemers pers. comm.
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Leptotes section

<i>Leptotes pirithous</i> ^d	2 ^{**}	indet.	Hinton 1951, Clark & Dickson 1971, Munguira, pers. comm.
<i>L. webbianus</i> °	0/1 ^{**}	?	Wiemers & Schurian, pers. comm. (lab.)

Castalius section

<i>Tarucus rosaceus</i>	3 ^{**}	<i>Plagiolepis pygmaea</i> <i>Camponotus sicheli</i> <i>Monomorium salomonis</i>	Chapman & Buxton 1919, Rojo de la Paz, pers. comm.
<i>T. theophrastus</i>	3 ^{**}	indet.	Baz 1988
<i>T. balkanicus</i>	3*(*)	indet.	Wiltshire 1945, 1948

Zizeeria section

<i>Zizeeria knysna</i> ^d	3 ^{**}	<i>Tapinoma</i> <i>melanocephalum</i>	Warnecke 1932/33, Clark & Dickson 1971
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<i>Cupido</i> section			
<i>Everes argiades</i> ^d	2**	indet.	Warnecke 1932/33
<i>E. decoloratus</i>	(2**)	?	no record
<i>E. alcetas</i>	(2)**	?	Elferrich, pers. comm. (lab.), Martín Cano 1982
<i>Cupido minimus</i>	3*	<i>Lasius alienus</i> <i>Formica fusca</i> <i>F. rufibarbis</i> <i>Plagiolepis vindobonensis</i> <i>Myrmica rubra</i>	Malicky 1969b, Baylis & Kitching 1988
<i>C. lorquinii</i>	3*	<i>Plagiolepis pygmaea</i> <i>Tapinoma nigerrimum</i>	Munguira & Martín 1989, Munguira, pers. comm.
<i>C. osiris</i>	3**	<i>Lasius alienus</i> + indet.	Malicky 1969b, SBN 1987
<i>Azanus jesous</i> ^d	3**	indet.	Bell 1915, Clark & Dickson 1971
<i>Lycaenopsis</i> section			
<i>Celastrina argiolus</i>	2**	<i>Lasius niger</i> <i>L. alienus</i> <i>L. fuliginosus</i> <i>Camponotus japonicus</i> <i>C. nearcticus</i> <i>Formica subsericea</i> <i>F. truncorum</i> <i>Myrmica</i> sp.	Malicky 1969b, Harvey & Webb 1980, Kitching & Luke 1985, Emmet & Heath 1990
<i>Glauopsyche</i> section			
<i>Glauopsyche alexis</i>	3**	<i>Lasius alienus</i> <i>Formica pratensis</i> <i>F. fusca</i> <i>F. cinerea</i> <i>F. nemoralis</i> <i>F. subrufa</i> <i>Camponotus aethiops</i> <i>C. maxiliensis</i> <i>Myrmica scabrinodis</i> <i>Crematogaster auberti</i> <i>Tapinoma erraticum</i> <i>Camponotus foreli</i> <i>C. cruentatus</i> <i>C. micans</i>	Malicky 1969b, Martín Cano 1981, SBN 1987
<i>G. melanops</i>	3**	<i>C. sylvaticus</i> <i>Myrmica sabuleti</i> <i>M. scabrinodis</i>	Malicky 1969b, Martín Cano 1981
<i>Maculinea arion</i>	4*	<i>Myrmica sabuleti</i> <i>M. scabrinodis</i>	Thomas et. al. 1989
<i>M. teleius</i>	4*	<i>Myrmica scabrinodis</i> <i>M. rubra</i> <i>M. vandeli</i> <i>M. sabuleti</i>	Thomas et al. 1989
<i>M. nausithous</i>	4*	<i>Myrmica rubra</i> <i>M. scabrinodis</i>	Thomas et al. 1989
<i>M. alcon</i>	4*	<i>Myrmica ruginodis</i> <i>M. rubra</i> <i>M. scabrinodis</i>	Thomas et al. 1989
<i>M. rebeli</i>	4*	<i>Myrmica schencki</i> <i>M. sabuleti</i> <i>M. scabrinodis</i> <i>M. sulcinodis</i>	Liebig 1989 (lab.) Thomas et al. 1989, Jutzeler 1989b

<i>Jolana jolas</i>	2*	<i>Tapinoma erraticum</i> + indet.	Warnecke 1932/33, Malicky 1969b, Schurian, pers. comm.
<i>Turanana panagaea</i> ¹	?	?	no record
<i>Pseudophilotes schiffermuelleri</i>	(2)**	?	no record
<i>Ps. baton</i>	2**	<i>Lasius alienus</i> <i>Myrmica scabrinodis</i>	Malicky 1969b, Blab & Kudrna 1982
<i>Ps. panoptes</i>	(2**)	?	Nel 1982
<i>Ps. barbagiae</i>	(2**)	?	no record
<i>Ps. abencerragus</i>	(2**)	?	Martín Cano 1982
<i>Ps. bavius</i>	2*(*)	indet.	König 1988
<i>Scolitantides orion</i>	3**	<i>Camponotus vagus</i> <i>C. aethiops</i> <i>Tapinoma erraticum</i> + indet.	Chapman 1915c, Malicky 1969b
<i>Polyommatus</i> section			
<i>Chilades trochylus</i> ⁴	3**	<i>Prenolepis</i> spp. <i>Pheidole quadrispinosa</i> <i>Iridomyrmex</i> sp.	Malicky 1969b, Clark & Dickson 1971, Wasserthal, pers. comm.
<i>Plebejus argus</i>	3/4**	<i>Lasius niger</i> <i>L. alienus</i> <i>Formica cinerea</i> ??	Kitching & Luke 1985, C. Thomas 1985, Mendel & Parsons 1987, Jutzeler 1989d, Ravenscroft 1990
<i>P. vogelii</i>	(3**)	?	no record
<i>P. (Plebejides) martini</i>	3**	<i>Crematogaster</i> sp.	Rojo de la Paz, pers. comm.
<i>P. (P.) trappi</i>	3**	<i>Formica lugubris</i> <i>F. lemani</i>	SBN 1987, Schurian & Jutzeler, pers. comm.
<i>P. (P.) hespericus</i>	3**	<i>Formica cinerea</i> <i>F. subrufa</i> <i>Plagiolepis pygmaea</i> <i>P. schmitzi</i> <i>Camponotus cruentatus</i> <i>C. foreli</i> <i>C. sylvaticus</i> <i>Crematogaster auberti</i>	Munguira & Martín 1989a, Munguira, pers. comm.
<i>P. (P.) sephirus</i>	3**	<i>Lasius</i> near <i>alienus</i> ⁹ <i>Formica pratensis</i> <i>Camponotus aethiops</i> <i>Tetramorium</i> near <i>caespitum</i> ⁹	Bálint & Kertész 1990, own observations
<i>P. (Lycaeides) idas</i>	3/4**	<i>Formica cinerea</i> <i>F. selysi</i> <i>F. exsecta</i> <i>F. lemani</i> <i>F. pressilabris</i> <i>F. lugubris</i> <i>F. lefrancoisi</i> <i>F. fusca</i> ?	Malicky 1969b, SBN 1987, Jutzeler 1989c, 1990
<i>P. (L.) argyrogynomon</i>	3**	<i>Lasius alienus</i> <i>L. niger</i> <i>Myrmica scabrinodis</i> <i>M. sabuleti</i>	Malicky 1969b, Blab & Kudrna 1982
<i>P. (Kretania) eurypilus</i> ¹	?	?	no record
<i>P. (K.) psylorita</i>	?	?	Hemmersbach 1989, Leighé et al. 1990
<i>P. (Vacciniina) optilete</i>	0	—	Malicky 1969b

<i>Polyommatus (Aricia) agestis</i>	3**	<i>Lasius alienus</i> <i>L. flavus</i> <i>Myrmica sabuleti</i> <i>Lasius</i> sp.	Jarvis 1958/59, Kitching & Luke 1985, Emmet & Heath 1990, Schurian, pers. comm.
<i>P. (A.) artaxerxes</i>	3**	<i>Lasius niger</i>	Malicky 1969b, SBN 1987
<i>P. (A.) cramera</i>	(3**)	?	no record
<i>P. (A.) morronensis</i>	3**	<i>Crematogaster auberti</i> <i>Tapinoma erraticum</i> <i>T. nigerrimum</i>	Munguira & Martín 1988
<i>P. (A.) nicias</i>	(3)**	?	Warnecke 1932/33
<i>P. (A.) anteros</i>	(3**)	?	no record
<i>P. (A.) eumedon</i>	3**	<i>Myrmica</i> sp.	Malicky 1969b, Weidemann 1986, SBN 1987, Schurian, pers. comm.
<i>P. (Albulina) orbitulus</i>	(2)**	?	Warnecke 1932/33, SBN 1987
<i>P. (Agriades) glandon</i>	0	—	Malicky 1969b, SBN 1987
<i>P. (A.) zuellichi</i>	0	—	Munguira & Martín 1989
<i>P. (A.) pyrenaicus</i>	0	—	Chapman 1915a
<i>P. (A.) dardanus</i>	(0)	—	no record
<i>P. (A.) aquilo</i>	(0)	—	no record
<i>P. (Agrodiætus) damon</i>	3**	<i>Lasius niger</i> <i>Formica pratensis</i>	Warnecke 1932/33, SBN 1987
<i>P. (A.) iphigenia</i>	(3**)	?	Malicky 1969b
<i>P. (A.) dolus</i>	(3**)	?	no record
<i>P. (A.) ainsae</i>	(3**)	?	Martín Cano 1982
<i>P. (A.) admetus</i>	(3)**	?	Martín Cano 1982
<i>P. (A.) fabressei</i>	(3)**	?	Warnecke 1932/33
<i>P. (A.) aroanensis</i>	(3**)	?	Martín Cano 1982,
<i>P. (A.) ripartii</i>	3**	indet.	Munguira, pers. comm.
<i>P. (A.) humedasae</i>	(3)**	?	no record
<i>P. (A.) thersites</i>	3**	<i>Lasius alienus</i> <i>Myrmica scabrinodis</i> <i>Tapinoma erraticum</i>	Rehfous 1954, Malicky 1969b, Schurian, pers. comm.
<i>P. (Cyaniris) semiargus</i>	3**	<i>Lasius</i> sp.	Weidemann 1986
<i>P. (C.) antiochena</i>	(3**)	?	no record
<i>P. (Lysandra) dorylas</i>	3**	<i>Formica cinerea</i> <i>Lasius alienus</i> <i>Myrmica scabrinodis</i>	Rehfous 1954, Weidemann 1986, SBN 1987
<i>P. (L.) golgus</i>	3**	<i>Tapinoma nigerrimum</i>	Munguira & Martín 1989b
<i>P. (L.) nivescens</i>	3**	<i>Tapinoma nigerrimum</i>	Munguira & Martín 1989b
<i>P. (L.) atlantica</i>	(3**)	?	no record
<i>P. (L.) amandus</i>	3**	<i>Lasius niger</i>	Hornemann, pers. comm.
<i>P. (L.) escheri</i>	3**	<i>Formica cinerea</i> <i>Myrmica specioides</i>	Chapman 1915b, SBN 1987, own observ.
<i>P. (L.) coelestina</i>	(3**)	?	no record
<i>P. (L.) coridon</i>	3**	<i>Lasius niger</i> <i>L. alienus</i> <i>L. flavus</i> <i>L. fuliginosus</i> (???)	Malicky 1969b, Kitching & Luke 1985, Fiedler 1987, Fiedler & Rosciszewski 1990, own observ.
		<i>Plagiolepis vindobonensis</i>	
		<i>Formica rufa</i>	
		<i>Myrmica scabrinodis</i>	
		<i>M. sabuleti</i>	
		<i>M. schencki</i>	
		<i>Tetramorium caespitum</i>	

<i>P. (L.) hispanus</i>	3**	<i>Plagiolepis pygmaea</i>	Maschwitz et al. 1975, Schurian, pers. comm.
<i>P. (L.) albicans</i>	3**	indet.	Schurian, pers. comm.
<i>P. (L.) bellargus</i>	3**	<i>Lasius alienus</i> <i>L. niger</i> <i>Plagiolepis pygmaea</i> <i>Myrmica sabuleti</i> <i>M. scabrinodis</i> <i>Tapinoma erraticum</i>	Malicky 1969b, Blab & Kudrna 1982, Kitching & Luke 1985, Jutzeler 1989e
<i>P. (L.) punctiferus</i>	3**	<i>Monomorium salomonis</i> <i>Crematogaster scutellaris</i>	Schurian & Thomas 1985
<i>P. (Meleageria) daphnis</i>	3**	<i>Lasius alienus</i> <i>Formica pratensis</i> <i>Tapinoma erraticum</i>	Schurian, pers. comm. & own obs.
<i>P. (Polyommatus) icarus</i>	2/3**	<i>Lasius alienus</i> <i>L. flavus</i> <i>L. niger</i> <i>Formica subrufa</i> <i>F. cinerea</i> ? <i>Plagiolepis pygmaea</i> <i>Myrmica sabuleti</i>	Malicky 1969b, Martín Cano 1984, Kitching & Luke 1985, SBN 1987, Jutzeler 1989d, Emmet & Heath 1990
<i>P. (P.) erooides</i> ^f	(3**)	?	no record
<i>P. (P.) eros</i>	3**	<i>Formica lemani</i> <i>Myrmica gallienii</i>	Jutzeler 1989a

Footnotes to Table 1:

^a Only two (independent?) old records. In the extensive literature about this locally endangered species and in recent textbooks, no mention of any ant-associations is given. Like all other European *Lycaena* species for which appropriate information is available, *L. dispar* is probably not truly myrmecophilous.

^b In laboratory experiments larvae of *L. ottomanus* were rather attractive to *Lasius niger* (Elfferich, pers. comm.).

^c Only one very old and doubtful record of an ant-association; see Fiedler (1990b) for detailed discussion.

^d Information concerning myrmecophily only available from outside Europe.

^e Wiemers observed no ants attending young larvae of *L. webbianus* in the field. Schurian, during his laboratory rearing, offered mature larvae to German *Lasius niger*. First the larvae were rather unattractive, but after some time they were palpated by the ants and the DNO was active. Thus the species may be at least weakly myrmecophilous.

^f Larval biology apparently unknown.

^g The *Lasius* workers collected in Hungary belong to a new species of the *alienus* group with distinct pubescence on the clypeus (det. B. Seifert). The species will be described by Seifert. Workers of the *Tetramorium caespitum* complex from Hungary cannot be determined with certainty; sexuals would be required.

Table 2: Numbers and percentages of facultatively (category 1-3) or obligately (category 4) myrmecophilous, and of myrmecoxenous (category 0) lycaenid species in Europe and North West Africa. The first table (a) is based exclusively on certain field observations; species whose larval biology is insufficiently known are excluded. The second table (b) is based on all assignments given in Table 1 (i.e. degrees of myrmecophily deduced from the situation in closely related species or from the presence of larval ant-organs are included).

a)

Tribus	not ant-associated	facultatively ant-associated	obligately ant-associated
Aphnaeini	-	1	3
Lycaenini	9	-	-
Theclini	-	2	-
Eumaeini	4	6	-
Polyommatini	4	46	7
total: 82 (100 %)	17 (20.7 %)	55 (67.1 %)	10 (12.2 %)

b)

Tribus	not ant-associated	facultatively ant-associated	obligately ant-associated
Aphnaeini	-	2	3
Lycaenini	13	-	-
Theclini	-	3	-
Eumaeini	4	7	-
Polyommatini	6	73	7
total: 118 (100 %)	23 (19.5 %)	85 (72.0 %)	10 (8.5 %)